Resilience and stability of a pelagic marine ecosystem

Lindegren, Martin ; Checkley, David M.; Ohman, Mark D.; Koslow, J. Anthony; Goericke, Ralf

Published in:
Proceedings of the Royal Society B: Biological Sciences

Link to article, DOI:
10.1098/rspb.2015.1931

Publication date:
2016

Document Version
Publisher's PDF, also known as Version of record

LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 00, 2016, 00–00

doi: 10.1002/lno.10249

Carbon export by vertically migrating zooplankton: an optimal behavior model

Agnethe N. Hansen*, André W. Visser
VKR Centre for Ocean Life, National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund, Denmark

Abstract

Through diel vertical migration (DVM), zooplankton add an active transport to the otherwise passive sinking of detrital material that constitutes the biological pump. This active transport has proven difficult to quantify. We present a model that estimates both the temporal and depth characteristic of optimal DVM behavior based on a trade-off between feeding opportunity and predation risk; factors that vary with latitude, time of year, and the size of the migrating animal. This behavioral component, coupled to a nutrient-phytoplankton-zooplankton (NPZ) productivity model provides estimates of the active transport of carbon by different size fractions of the migrating zooplankton population as function of time and space. The approach is motivated by the difficulty in incorporating behavioral aspects of carbon transport into large scale carbon budgets of the world's oceans. The results show that despite their lower abundance, large zooplankton (length circa 1–2 mm) migrate deeper and transport approximately twice as much carbon as do the smaller zooplankton (length circa 0.2–0.3 mm). In mid- latitudes (~30°N to ~45°N), where pronounced spring blooms are observed, up to 20% more carbon is transported than at either equatorial or boreal latitudes. We estimate that the amount of carbon transported below the mixed layer by migrating zooplankton in the North Atlantic Ocean constitutes 27% (16–30%) of the total export flux associated with the biological pump in that region.

The oceans play a major role in regulating global climate, one aspect of which is their potential to remove anthropogenic CO_2 from the atmosphere. Primary producers assimilate CO_2 in the euphotic zone to produce organic matter, a fraction of which is exported to the deep ocean as detrital material (e.g., sinking as aggregates, marine snow, and fecal pellets). On its way from the surface mixed layer through the meso-pelagic ocean 80–90% of this detrital material is remineralized (Martin et al. 1987; Burd et al. 2010; Giering et al. 2014). The remaining fraction reaches the depths where it is sequestered in the ocean bottom or in deep circulation currents. This mechanism is part of the biological pump which together with the solubility pump are the main sequesters of carbon from the atmosphere into the deep ocean (Volk and Hoffert 1985; Longhurst and Harrison 1989; Ducklow et al. 2001; Boyd and Trull 2007).

The biological pump is strongly regulated by the resident zooplankton community (Steinberg et al. 2000). Mesozooplankton in particular process up to 40% of the primary production, either in direct grazing on phytoplankton or feeding on micro-zooplankton consumers (Frangoulis et al. 2005), producing fast sinking fecal pellets that contribute significantly to export flux (Honjo and Roman 1978; Smith et al. 2009). Additional processes mediated by zooplankton include feeding and disruption of particle fluxes (Alldredge and Silver 1988; Steinberg et al. 2008b), and active carbon transport by vertical migrators (Dam et al. 1995; Steinberg et al. 2002; Jónasdóttir et al. 2015). With regards to the latter, many meso-zooplankton grazers perform diel vertical migration (DVM), feeding in the surface at night and finding refuge from visual predators at depth during sunlight hours (Longhurst 1976). This behavior can bring them below the euphotic zone where they leave behind excreted organic matter and respired CO_2 (Longhurst et al. 1990; Steinberg et al. 2000), thus contributing to the export flux with an active component. Despite its importance for the biological pump and the export of carbon from the surface ocean, this active component remains poorly quantified (Steinberg et al. 2000, 2001), particularly in terms of the global carbon budget. There is a need to investigate the role of zooplankton DVM in the sequestering of carbon from the

Additional Supporting Information may be found in the online version of this article.

*Correspondence: agno@aqua.dtu.dk

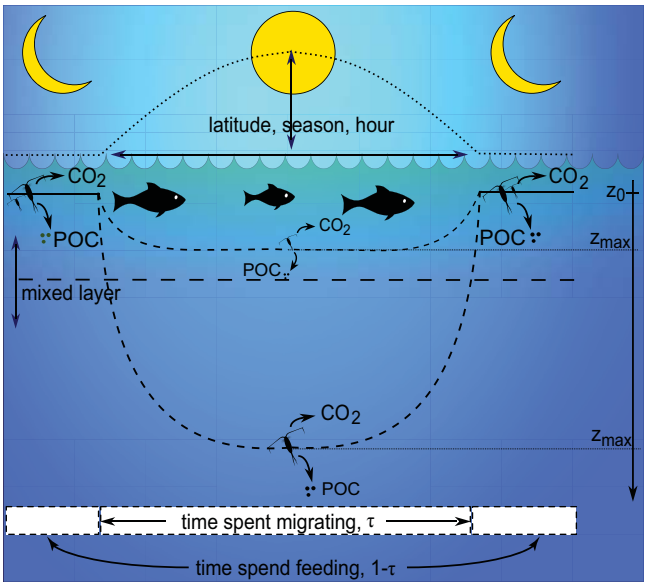

Fig. 1. A conceptual overview of the diel vertical migration (DVM) model. During hours of darkness, zooplankton graze in the surface, but retreat to depth during day light hours as they become more vulnerable to visual predators. The zooplankton can vary the time they spend on migration (τ) and their maximum migration depth (z_{max}) to optimize their fitness as a trade-off between feeding, cost of migration and mortality risk; factors that can be expected to vary with latitude, time of year, and zooplankton size. The zooplankton excrete and respire carbon, which in this model is assumed to occur continuously on the migration path. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

atmosphere, especially as the net primary production is predicted to decrease in response to climate change with up to 20% by 2100 (Steinacher et al. 2010). Changes in the ocean productivity and the zooplankton community might have large implications for the sequestration of CO_2 from the atmosphere and hence the global climate (Sarmiento et al. 1998; Smith et al. 2009).

Several studies have observed the active flux of organic and respiratory carbon from migrating zooplankton (Longhurst et al. 1990; Morales 1999; Steinberg et al. 2000; Stukel et al. 2013). However, all of these are based on limited spatial and temporal information which is susceptible to seasonal and latitudinal variations in both primary and secondary production (Burd et al. 2010). Therefore, extrapolation of the findings into global oceanic carbon budgets remains a challenge. Using a dynamic modeling approach based on the trade-off between gain from feeding and risk of mortality we predict the optimal DVM behavior of zooplankton under seasonally varying light and food conditions. Subsequently, we estimate how this impacts the active carbon transport by migrating animals. It is applied to the North Atlantic Ocean as an example, but is otherwise general. The model is simple enough to be implemented into ocean general circulation models (OGCMs), providing regional and seasonal estimates of the active carbon transport by migrating zooplankton in the global assessments of CO_2 dynamics.

Method

An optimal behavior model of diel vertical migration

The model presented here considers the trade-off between gaining energy for growth and reproduction and avoiding predation. This trade-off has been modeled several times before (Gilliam and Fraser 1987; Houston et al. 1993; De Robertis 2002; Visser 2007) and concerns the classic dilemma that a high energy gain nearly always comes with a high predation risk (Lima and Dill 1990; Houston et al. 1993). A simple heuristic that reflects this trade-off is Gilliam's rule (Gilliam and Fraser 1987; Kristiansen et al. 2009; Sainmont et al. 2015), where optimal behavior can be estimated as that which maximizes net energy gain over mortality rate. In this way, the zooplankton can optimize their fitness by performing DVM (Fig. 1). Applying Gilliam's rule to migrating zooplankton, the functional form of fitness depends on the depth of migration (z_{max}) and the fraction of the day spent migrating (τ) (Eq. 1):

$$f(z_{max},\tau)=(g(1-\tau)-c(z_{max},\tau))/\mu(z_{max},\tau) \quad (1)$$

where g is the energy gain (J d^{-1}), c is the energetic cost (J d^{-1}) and μ is the mortality rate (d^{-1}). Hence, f is an estimate of the zooplankton fitness in terms of net energy gain (J) during its expected lifetime assuming an unchanging environment (i.e., the animal has no knowledge of future change) (Gilliam and Fraser 1987; De Robertis 2002; Sainmont et al. 2015). The energetic gain from feeding can be written as

$$g(1-\tau)= e_p\beta c_{surf}\varepsilon_{assim}(1-\tau) \quad (2)$$

depending on the fraction of a day the zooplankton spend grazing at the surface, $1-\tau$. The fraction of day the zooplankton spend migrating (down from the surface, resting at depth, and returning to surface) will be referred to as "migration time" (Fig. 1). e_p is the energy content of the prey (J gC^{-1}), β is the maximum clearance rate ($\beta=ar^3$ (m^3 d^{-1}), where r is the radius of the zooplankton (m) and $a \approx 4 \times 10^6$ d^{-1}, which is an empirical scaling of the clearance rate to the volume of the organism (Kiørboe and Jiang 2013)). c_{surf} is the phytoplankton abundance (gC m^{-3}) and ε_{assim} is the assimilation efficiency. We use a Hollings type I functional response with a maximum ingestion rate set to 200% of body carbon per day if the zooplankton is feeding full time. This parameter will typically depend on the diet of the zooplankton; Besiktepe and Dam (2002) found variations between 92–610% of body carbon consumed per day in *Acartia tonsa* fed on different species of phytoplankton. As neither zooplankton nor phytoplankton species are modeled explicitly, 200% per day seems a reasonable estimate.

The mortality μ is dependent on light exposure (Aksnes and Giske 1993; De Robertis 2002) (Eq. 3). Also, zooplankton are observed to attempt to follow isolumes in their migration to depth (Heywood 1996; Sainmont et al. 2014), which makes a proportionality to light exposure a realistic assumption regarding mortality. Specifically,

$$\mu(z_{\max}\tau) = \mu_0\left(1+m_{\text{fac}}\hat{L}(z_{\max},\tau)\right) \quad (3)$$

where μ_0 is the background mortality (d^{-1}), which is the mortality experienced in total darkness (i.e., mortality not by visual predators, starvation or disease, but just the inverse of the expected lifetime of a zooplankter). $\hat{L}(z_{\max},\tau)$ is the daily mean light exposure of a zooplankton on its path of migration (see Supporting Information for details on calculation). It is assumed that the risk of mortality is 20 times higher in maximum daylight than in darkness, hence the light risk factor $m_{fac}=20$. De Robertis (2002) has used a similar argument in his model of the timing of DVM, setting the risk of mortality from visual predators 10 times higher than from all nonvisual sources combined. In this model, we assume visual predation risk to be size independent. However, there are processes that place an allometric scaling on mortality. Conversely, while larger preys are visually more conspicuous (Aksnes and Giske 1993), they also have greater escape ability as well as fewer predators (Hirst and Kiørboe 2002). Rather than make this an ambiguous model effect, we choose to use a size neutral mortality risk depending solely on light level.

As the zooplankton migrate vertically there is an associated energetic cost c (J d^{-1}) depending on the maximum depth of migration, $z_{\max}$, and migration time, τ:

$$c(z_{\max}\tau) = 1/\tau q k(|z_{\max}-z_0|)^2 \quad (4)$$

where q is the cost of swimming. q is a function of zooplankton size (radius, r), $q(r)=6\pi r\nu_{\text{kin}}/\varepsilon_{\text{swim}}$ (W m^2 s^{-2}), where ν_{kin} is the kinematic viscosity of seawater and $\varepsilon_{\text{swim}}$ is the swimming efficiency, here set to 1% (Visser 2007). z_0 is the grazing depth (m) and k is a constant arising from integrating along the migration path (ζ, See Eq. A1 and A7 in Supporting Information), which relates the cost to the swimming effort so that higher speed comes at a higher energy cost (Visser 2007).

Table 1 provides values and descriptions of model parameters.

Table 1. Overview of constants and parameters.

Parameter	Description	Value	Unit
f	Fitness measure		J
c	Cost of migration		J d^{-1}
g	Gain from grazing		J d^{-1}
μ	Total mortality		d^{-1}
τ	Fraction of day spent migrating		—
$z_{\max}$	Maximum migration depth		m
$\varepsilon_{\text{assim}}$	Assimilation efficiency	2/3	—
ε_c	Excretion and respiration fraction	1/3	—
z_0	Grazing depth	10	m
m_{fac}	Mortality factor	20	—
μ_0	Background mortality	0.05	d^{-1}
$\varepsilon_{\text{swim}}$	Swimming efficiency	0.01	—
ν_{kin}	Kinematic viscosity of water	1.3×10^{-6}	m^2 s^{-1}
e_{p}	Energy content of prey	4200	J gC^{-1}
r	Radius of organism	0.1–1	mm
k	Constant		—
β	Maximum clearance rate		m^3 d^{-1}
a	Clearance rate scaling	4×10^6	d^{-1}
q	Drag coefficient		W s^{-2} m^{-2}
$\hat{L}$	Mean light exposure		—
τ_{ML}	Fraction of day spent below ML		—
c_{surf}	Surface organic carbon		mg C m^{-3}
Z	Migrating individuals		ind m^{-2}

Application of the model

To provide the DVM model with estimates of phytoplankton abundance, we use a simple nutrient-phytoplankton-zooplankton (NPZ) model. The set-up is identical to the one made by Evans and Parslow (1985), with the deep ocean nutrient concentration tuned (from 10 mM N m^{-3} to 4 mM N m^{-3}) to keep the resulting plankton abundance realistic (peak values of the order 100 mgC m^{-3}). The NPZ model is forced with a growth rate based on an annual light cycle (as a function of latitude) and a time-series of mixed layer depth (see Supporting Information for further explanation and visualization of the NPZ model results). The model is adjusted to simulate the North Atlantic conditions and reproduces the magnitude and timing of the spring blooms observed in northern latitudes (Colebrook 1979; Townsend et al. 1994; Behrenfeld 2010). In keeping with the NPZ model construction, the simulated zooplankton population is assumed to be herbivorous with their growth fuelled only from grazing on phytoplankton. While not explicitly considered in this simple model, part of the zooplankton diet also consists of mirco-zooplankton consumers, a process that is to some extent modeled in the zooplankton net grazing rate. It is assumed that the zooplankton population consist of copepods, such as e.g., *Calanus* spp., which are often dominating the zooplankton community and typically exhibit a strong DVM behavior (Hays 1996; Dale and Kaartvedt 2000; Irigoien et al. 2004).

The optimal migration strategy is found by maximizing relative fitness, f (Eq. 1), with regards to migration depth ($z_{\max}$) and migration time (τ) for given environmental conditions, both physical and biotic. Different optimal strategies will emerge for different environmental conditions. The optimal $z_{\max}$ and τ are used to estimate how much carbon is

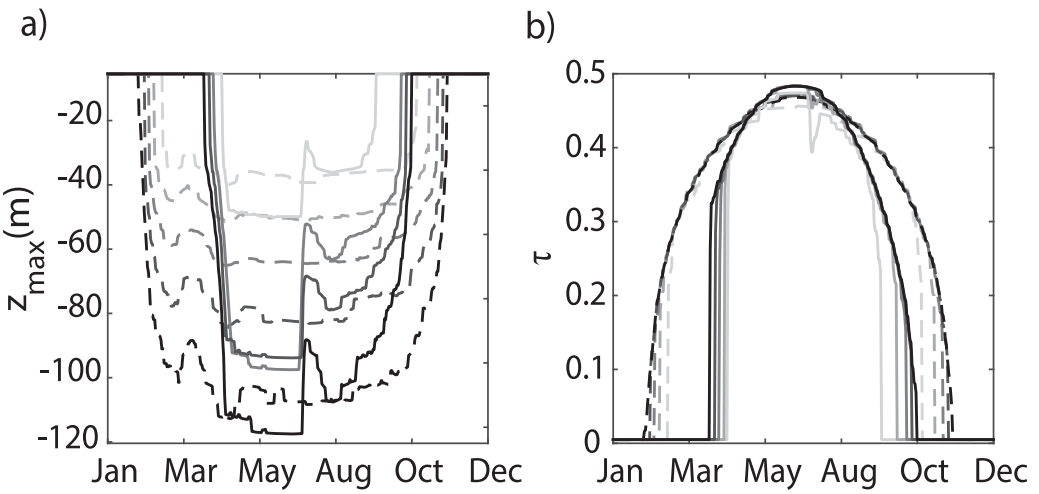

Fig. 2. (a) The optimal migration depth ($z_{\max}$) and (b) the optimal migration time (τ) as a fraction of the day. The shading of the black indicates the five zooplankton size classes (0.2–2 mm, the largest size class in black). Iceland is in solid lines and Bermuda is in dashed lines.

consumed in the surface and subsequently excreted and respired below the mixed layer, Flux_{ML} (mg C m^{-2} d^{-1}), by migrating zooplankton. That is

$$\text{Flux}_{\text{ML}} = g\left(z_{\max,\text{opt}}, \tau_{\text{opt}}\right) 1/e_{\text{p}} Z \varepsilon_{\text{c}} \tau_{\text{ML}} \qquad \text{(Eq. 5)}$$

where $g\left(z_{\max,\text{opt}}, \tau_{opt}\right)$ is the gain (J d^{-1} ind^{-1}) achieved when choosing the optimal migration strategy, e_{p} (J gC^{-1}) is the energy content of the phytoplankton and Z (ind m^{-2}) is the number of migrating zooplankton in the water column (estimated using carbon contents (mg C ind^{-1}) derived from regressions of zooplankton length to carbon content from Mauchline (1998)). Z is an estimate from the NPZ model and it is assumed that all zooplankton perform optimal DVM. It is assumed that the fraction of the ingested carbon that is excreted or respired is constant throughout the day, and that there are no temperature or pressure dependence on this. τ_{ML} is the fraction of a day spend below the mixed layer (we define the mixed layer as it is used in the NPZ model (Supporting Information Fig. S1)). This method of estimating carbon export is similar to the approach applied by Dam et al. (1995) and Steinberg et al. (2000) who estimated zooplankton respiratory carbon flux across the mixed layer from observations on migrant biomass and respiration rates assuming equal time spent above and below the mixed layer (i.e., $\tau_{ML} = 0.5$). In contrast, in our model τ_{ML} is an emergent property of optimal DVM behavior, and can vary substantially as a function of latitude, time of year, zooplankter size, and phytoplankton biomass.

To predict the amount of carbon transported vertically, the vertical migration distance is separated into 20 m intervals (referred to as depth bins). The optimal gain and the cost depend on the size of the organism. For simplicity, we assume the zooplankton biomass is distributed according to a logarithmic size spectrum ranging 0.2–2 mm (Sheldon and Parsons 1967) which is split into five different size-classes. In reality, zooplankton size compositions will vary both over season and latitude, but this assumption provides some estimate of zooplankton size distribution in natural populations. During the rest of the study, organisms in the high end of this size spectrum (ca. 1–2 mm) are referred to as large zooplankton and those towards the low end (0.2–ca. 0.3 mm) as small zooplankton.

To illustrate the predictions of the model in detail, two latitudes in the North Atlantic are selected; 31°N (Bermuda) and 60°N (Iceland). These sites are chosen to represent two different annual cycles; Iceland has a phytoplankton bloom in spring, followed by a zooplankton bloom (Colebrook 1979), while the phytoplankton abundance at Bermuda is more constant throughout the year (less than an order of magnitude changes in abundance (Steinberg et al. 2001)).

Results

Optimal migration patterns

Due to the low phytoplankton abundance off Iceland from October to April, the model predicts no migration in this period, and zooplankton begin migrating as the bloom is initiated (Fig. 2). At Bermuda, zooplankton perform DVM during most of the year, except for the winter months from November to January (Fig. 2). During winter, phytoplankton abundance is so low that it is not energetically feasible for zooplankton to migrate. In addition, light levels are low during winter at Iceland which diminishes visual predation risk and reduces the need to migrate.

During the spring bloom, zooplankton migrate deeper than the rest of the year (Fig. 2a, solid lines) as their food resources becomes more abundant and they can afford to spend energy on migrating deeper. The contour lines in Fig. 3 provide an estimate of the sensitivity of fitness to actual

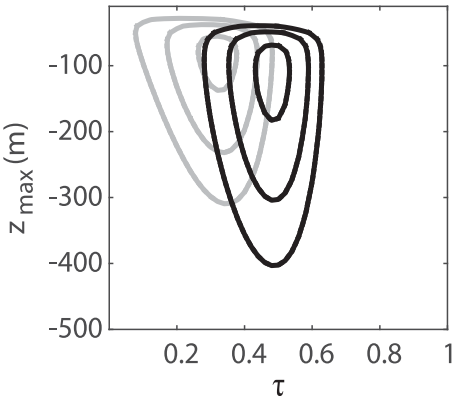

Fig. 3. Contours of the fitness surface indicating 99%, 95%, and 90% of optimal fitness for a zooplankton from the large size class (1–2 mm). Black contours represent a day during the spring bloom and grey contours a day during fall for the Iceland site.

migration strategy. The stretching of fitness contours with depth (Fig. 3) is a consequence of the exponential attenuation of light in the water column. This means that the relative increase in fitness for a migration depth interval is much greater in the surface than at depth.

Large zooplankton are consistently predicted to migrate deeper than smaller zooplankton (Fig. 2), as they are capable of acquiring more energy to spend on migration. Specifically, the energy gained from feeding has a cubic relation with zooplankton size (Eq. 2), while cost is has a linear dependence (Eq. 4), so that energetic gain from feeding can offset the cost of migration more readily for larger zooplankton. Consequently, large zooplankton can migrate deeper. The model predicts that large zooplankton migrate down to a maximum depth of 87–112 m from their grazing depth in the surface, giving them a net migration amplitude of up to 102 m (from z_0 to z_{max}) (Table 2).

Carbon transport by migrating zooplankton

As DVM occurs during most of the year at Bermuda, a larger amount of organic carbon is transported there compared to Iceland (Fig. 4). At Iceland, spring blooms are essential for the active transport, as almost all active flux occurs in the short period during the bloom where both phytoplankton and zooplankton abundances are high (Fig. 4a, left panel).

Large zooplankton have higher ingestion rates and they are responsible for transporting more than twice as much carbon as the small zooplankton (Fig. 4, right panels). This means that although there are considerably fewer individuals compared to smaller size classes (due to the logarithmic size spectrum), large zooplankton are more important; they migrate deeper and transport more carbon further away from the surface. This tendency is supported by observations that find large copepods migrating deeper and showing significantly stronger DVM than smaller ones (Wiebe et al. 1992; Hays et al. 1994). In this model, all size classes contribute to the active export flux, but due to their greater importance the large zooplankton (length ca. 1–2 mm) are responsible for almost 50% of the predicted transport below the mixed layer (Fig. 5).

Intermediate latitudes ($\sim$ 30°N to $\sim$ 45°N) have the highest active carbon transport (Fig. 5). This is a result of the relatively high annual productivity at these latitudes predicted by the NPZ model, exhibiting a significant spring bloom on top of phytoplankton concentrations above 10–20 mg C m^{-2} the rest of the year (Supporting Information Fig. S1). This combination results in approximately 20% higher active carbon export in latitudes $\sim$30°N to $\sim$45°N compared to the either boreal or equatorial latitudes (Fig. 5).

Integrating over the whole North Atlantic (0°N to 66°N) suggests a total active transport contribution to the export flux of 0.34 (0.2–0.37). In terms of the mean particulate organic carbon (POC) export flux of 1.27 Gt C yr^{-1} in the North Atlantic (Sanders et al. 2014), 27% (16–29%) is mediated through the transport by zooplankton DVM, an estimate that is in the same range as observations (Table 2).

Discussion

Optimal DVM

The predicted migration depths and amplitudes of the large zooplankton are comparable to observations of DVM of large meso-zooplankton (Longhurst et al. 1990; Heywood 1996; Irigoien 2004; Steinberg et al. 2008a; Sainmont et al. 2014) (Table 2). Irigoien et al. (2004) studied migration amplitudes of several different species and stages of species in the central Irish Sea; here, he found that adult copepods of the *Calanus* spp. have migration amplitudes above 70 m and smaller stages have migration amplitudes up to 40 m, when migrating from their night depth to their day refuge. In the North Pacific, Steinberg et al. (2008a) find that zooplankton (1–2 mm) have migration amplitudes of 129 m, which is also comparable to the model estimate (Table 2). Irigoien (2004) found in the central Irish Sea that large copepods (e.g., *Calanus* spp.) migrate deeper than small ones, which is consistent with one of the key patterns produced by the model (Fig. 2a). This pattern is also seen in the observations of zooplankton (0.3–5 mm) by Steinberg et al. (2008a) at the K2 and ALOHA stations in the North Pacific and by Wiebe et al. (1992) in a study of migration patterns of several copepod species in a warm-core ring of the Gulf Steam.

The model predicts very little size dependence on migration time (τ) although it seems that large zooplankton spend a slightly higher fraction of the day on migration than the small ones (Fig. 2b). In contrast, the study by De Robertis (2002) finds that large zooplankton descent earlier and ascent later than small ones, making them spend a larger fraction of the day on migration, a result quantitatively

Table 2. Specific results from the DVM model on optimal migration patterns and export flux. From Iceland results are calculated both from the spring bloom peak and the fall, but from Bermuda only yearly mean values are shown. Predicted optimal maximum migration depth is the predicted migration distance from surface to z_{max} and the estimate of migration amplitudes covers the distance from z_0 to the z_{max}. The time spent migrating is the time it takes the zooplankton to migrate from z_0 to the maximum depth bin. Estimates are generally based on the large zooplankton (ca. 1–2 mm), except from the zooplankton biomass, the migrant biomass and the active C flux estimates that contain all size classes (0.2–2 mm). In the model, all zooplankton are assumed to follow the optimal migration, therefore zooplankton biomass and migrant biomass estimates are equal. The export estimates are based on excreted and respired carbon transported below the mixed layer. The yearly flux estimates is shown with the estimate from 95% of the optimal fitness in parentheses (see Fig. 3).

	Iceland		Bermuda		
	Bloom	**Fall**	**Mean**	**Observation**	**Reference**
Zoop. biomass (mg C m^{-2})	2828	597	676	Up to 3000*	Lenz et al. (1993)
Phytop. density (mg C m^{-3})	305	17	17	10–80	Behrenfeld (2010)
Max. migration depth (m)	112	87	103	50–100	Longhurst et al. (1990), Heywood (1996)
				50–120	Sainmont et al. (2014)
Amplitude of migration (m)	102	77	93	50–70	Irigorien et al. (2004)
				129	Steinberg et al. (2008a)
Time spent migrating (min)	~60	~45	~70	30–60	Wiebe et al. (1992)
Gut passage time (min)	–	–	–	25–130	Mauchline (1998)
% copepod C ingested d^{-1}	104	87	105	5–130	Mauchline (1998)
				92–610	Besiktepe and Dam (2002)
% copepod C ex+resp d^{-1}	35	29	35	8–30	Longhurst et al. (1990)
Ingestion rate (mg C m^{-2} d^{-1})	2332	301	362	480 (1179)†	Dagg et al. (1982)
Migrant biomass (mg C m^{-2})	2828	597	676	97–536	Dam et al. (1995)
Active C flux (mg C m^{-2} d^{-1})	201	37	32	2.4–47.1	Stukel et al. (2013)
				0–9.9	Steinberg et al. (2000)
				4.2–40.6	Dam et al. (1995)
				2.8–8.8	Longhurst et al. (1990)
% of total flux	51‡	23§	20§	1.9–40.5	Stukel et al. (2013)
				18–70¶	Dam et al. (1995)
				0–39	Steinberg et al. (2000)
Active C flux (g C m^{-2} yr^{-1})	6.6 (4.9–7.0)		11.5 (5.4–13.1)	1.02–3.21¶	Longhurst et al. (1990)
				0.33–7.67‖	Morales (1999)
NA active C flux (Gt C yr^{-1})	0.34 (0.2–0.37)#			–	–
NA Active C flux/NA POC flux (%)	27 (16–29)#,**			6–22††	Longhurst et al. (1990)
				19–40	Morales (1999)

*From spring bloom 0–500 m meso-zooplankton biomass integration at 58°N in North Atlantic.
†Peak observation in parentheses.
‡Active C flux estimate of 201 mg C m^{-2} d^{-1} compared to a spring bloom POC flux (across 150 m) of ~ 400 mg C m^{-2} d^{-1} (Buesseler et al. 1992; Caron et al. 2004).
§Active C flux estimate compared to a mean POC flux of 161 mg C m^{-2} d^{-1} in North Atlantic (Sanders et al. 2014).
¶Only respiration.
‖Only defecation.
#Based on an estimate of the North Atlantic 0–66°N area of 3.62×10^{13} m^2.
**NA active C flux estimate compared to the mean North Atlantic POC export flux of 1.27 Gt C yr^{-1} (Sanders et al. 2014).
††Global estimate based on migrant respiratory flux below mixed layer.

supported by observations (Wiebe et al. 1992). This short-fall in our model may be due to the scaling of mortality risk to size, where large zooplankton are visually more conspicuous (Aksnes and Giske 1993; De Robertis 2002).

For large zooplankton, time spent migrating from the surface to the maximum depth is within the time interval for typical gut clearance rate of copepods (Table 2). In their study of DVM in the Gulf Stream, Wiebe et al. (1992) find that it typically takes about 30–60 min for a copepod to migrate back towards the surface from its day refuge. This is comparable to the time estimates of migration from the model (Table 2). Gut clearance over this time interval means

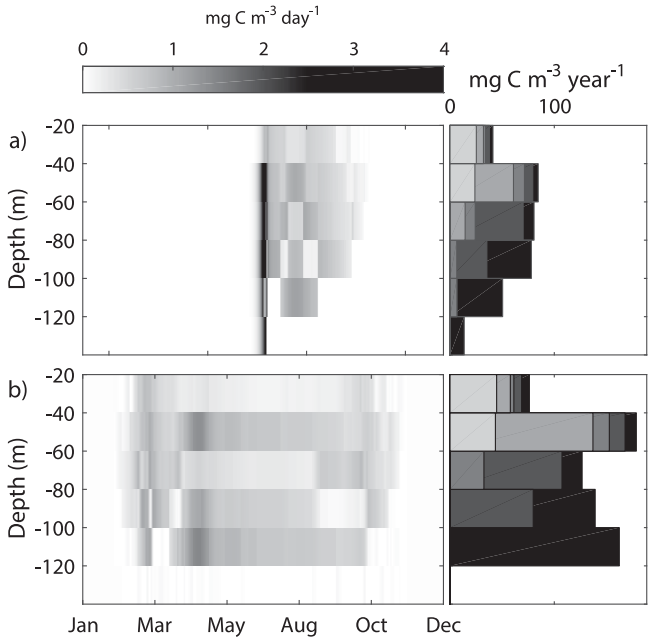

Fig. 4. Estimates of carbon respiration and excretion with depth; daily estimates left and yearly estimates right from (a) Iceland and (b) Bermuda. The different shades in the right panels show the contribution of zooplankton of the five size-classes (0.2–2 mm, the largest size class in black).

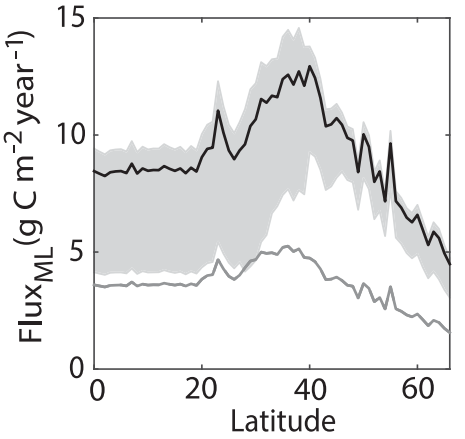

Fig. 5. Estimate of the total active transport of excreted and respired carbon integrated across all size classes (0.2–2 mm) to below the mixed layer at all latitudes ranging 0–66°N (solid line). The grey shading indicates the variance in transport associated with a 95% spread in relative fitness with regards optimal migration depth, and the grey line indicates the contribution of only the largest zooplankton size class (circa. 1–2 mm).

that the zooplanktons' gut is cleared as it reaches maximum depth, and therefore the excretion only occurs on half of the migration path and not continuously as assumed in the DVM model. This might lead to an overestimation of the active flux, but due to the large variation in the gut clearance rate for different species, sizes and life stages, it is unclear whether inclusion of the aspect would considerably improve the active flux estimates.

Export flux

Generally, the estimated ingestion and respiration and excretion rates are in the high end compared to observations (Table 2). These rates are related to the efficiency ε_c that is set to 1/3. Ideally this rate would vary, e.g., with ambient temperature and zooplankton diet (Dam and Peterson 1988; Besiktepe and Dam 2002) but to keep with the aim of the simplest possible model, this rate is assumed constant. As the predicted ingestion rates and consequently the excretion and respiration rates are in the high end results in the model overestimating the active flux.

Previous estimates of the active carbon flux as percentage of the POC flux have been made in the North Atlantic (Longhurst et al. 1990; Dam et al. 1995; Steinberg et al. 2000) and North Pacific (Stukel et al. 2013) based on observations over short time intervals. Compared to these, the model estimates are at the high end (Table 2), especially, the active flux at Iceland during spring bloom of 201 mg C m^{-2} d^{-1}. In the northern North Atlantic Caron et al. (2004) and Buesseler et al. (1992) find spring bloom POC flux across 150 m by which amounts to ~400 mg C m^{-2} d^{-1}. Compared to this observation, the model estimate from the spring bloom at Iceland constitutes ~50% (Table 2). Dam et al. (1995) found that the respiratory carbon flux from migrating zooplankton across 150 meters during spring constituted on average 34 (±16)% of the gravitational POC flux at Bermuda. At same location, Steinberg et al. (2000) find the migratory carbon flux ranging 0–39% of the mean POC flux. For comparison, the model estimates that 20–23% of the mean daily North Atlantic POC flux of 161 mg C m^{-2} d^{-1} (Sander et al. 2013) is from active transport from DVM (Table 2, when disregarding the bloom conditions). This indicates that while the model seems to overestimate some aspects, it performs well when estimating the proportional importance of the active flux.

Impacts of model dynamics and assumptions

The motivation for this study has been in part to demonstrate the proof-of-concept for the introduction of active carbon transport by migrating zooplankton into OGCM's as a dynamic element, an issue that is seen as a limiting factor in accurate representations of the biological pump (Steinberg et al. 2000). In this, we have demonstrated the feasibility of the approach and have verified the model results in terms of broad spatial and temporal patterns. There are, however, several points where the model can be improved. For instance, while allowing for a dynamic migration behavior in response to changes in the light and food availability, our model is not fully dynamic. The DVM model has no coupling back to the NPZ model. For instance, DVM will modulate the effective grazing pressure on phytoplankton. In addition, active transport by DVM removes nitrogen from the mixed layer

along with carbon, which in a fully dynamic model also would impact the phytoplankton growth. Likewise, there are game theoretic aspects to consider, where optimal behavior also depends on the emergent behavior of predators, prey and competitors (Sainmont et al. 2013). The DVM model also assumes no future change in conditions, either in the environment or the organism, which is the so-called myopic assumption (Sainmont 2015). In reality, the choices made by a zooplankter will affect its lifetime fitness (Mangel and Clark 1988; Houston and McNamarra 1999) as the organism grows and contends with seasonal variations. In this, both the state and the stage of the organism are important; is it hungry or full, is it trying to find a mate, is winter coming? Such aspects can influence the outcome of choices in ways not predicted by myopic optimal behavior based on Gilliam's rule.

The model incorporates a simple representation of zooplankton size that assumes a uniform distribution of biomass within logarithmic length classes. As well as latitudinal variations (San Martin et al. 2006), zooplankton size will reflect species succession and ontogeny through a seasonal cycle with small zooplankton dominating in early spring and fall and larger individuals dominating during the summer. Subsequently, variations in size distribution within the zooplankton community will introduce variations in the active carbon export, and would require a size structured zooplankton model (e.g., Ward et al. 2012) to be resolved.

Parameters like the background mortality (μ_0) and the mortality factor (m_{fac}) are in nature are very variable in time and space. There are also many issues that we have chosen to ignore in the model—for instance gut clearance, temperature effects on metabolism, maximum swimming speed, and micro-zooplankton prey. While these and other factors might add uncertainty to the model results, we stress that the aim of study is as much about producing general spatial and seasonal patterns of DVM and active carbon transport by zooplankton as it is about exact predictions in given locations.

Conclusion

We have demonstrated a general method by which the effects of DVM can be incorporated into models of carbon export. The method is dynamic in nature, being driven by the optimization of feeding opportunity against the risk of predation. The general patterns, both spatially and temporally, are in broad agreement with observations. The size of the zooplankton is resolved, and it appears that the greatest flux is driven by a small number of large animals.

The findings of this model study support earlier studies and suggest that the active transport of carbon by diel vertically migrating zooplankton is substantial and should be considered when making estimates of the oceans atmospheric carbon sequestration. Even more importantly, the model proposes a simple way to include the dynamics of the active transport into global scale carbon budgets.

References

Aksnes, D. L., and J. Giske. 1993. A theoretical model of aquatic visual feeding. Ecol. Modell. **67**: 233–250.

Alldredge, A. L., and M. W. Silver. 1988. Characteristics, dynamics and significance of marine snow. Prog. Oceanogr. **20**: 41–82. doi:10.1016/0079-6611(88)90053-5

Behrenfeld, M. J. 2010. Abandoning Sverdrup's critical depth hypothesis on phytoplankton blooms. Ecology. **91**: 977–989. doi:20462113

Besiktepe, S., and H. G. Dam. 2002. Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. Mar. Ecol.: Prog. Ser. **229**: 151–164. doi:10.3354/meps229151

Boyd, P. W., and T. W. Trull. 2007. Understanding the export of biogenic particles in oceanic waters: Is there consensus?. Progr. Oceanogr. **72**: 276–312. doi:10.1016/j.pocean.2006.10.007

Buesseler, K. O., M. P. Bacon, J. K. Cochran, and H. D. Livingston. 1992. Carbon and nitrogen export during the JGOFS North Atlantic bloom experiment estimated from ^{234}Th:^{238}U disequilibria. Deep-Sea Res. Part I **39**: 1115–1137. doi:10.1016/0198-0149(92)90060-7

Burd, A. B., and others. 2010. Assessing the apparent imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological activity: What the @$#! is wrong with present calculations of carbon budgets? Deep-Sea Res. Part II **57**: 1557–1571. doi:10.1016/j.dsr2.2010.02.022

Caron, G., C. Michel, and M. Gosselin. 2004. Seasonal contributions of phytoplankton and fecal pellets to the organic carbon sinking flux in the North Water (Northern Baffin Bay). Mar. Ecol.: Prog. Ser. **283**: 1–13. doi:10.3354/meps283001

Colebrook, J. M. 1979. Continuous plankton records: Seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. Mar. Biol. **51**: 23–32. doi:10.1007/BF00389027

Dagg, M. J., J. Vidal, T. E. Whitledge, R. L. Iverson, and J. J. Goering. 1982. The feeding, respiration, and excretion of zooplankton in the Bering Sea during a spring bloom. Deep-Sea Res. Part I **29**: 45–63. doi:10.1016/0198-0149(82)90060-7

Dale, T., and S. Kaartvedt. 2000. Diel patterns in stage-specific vertical migration of *Calanus finmarchicus* in habitats with midnight sun. ICES J. Mar. Sci. **57**: 1800–1818. doi:10.1006/jmsc.2000.0961

Dam, H. G., and W. T Peterson. 1988. The effect of temperature on the gut clearance rate constant of planktonic copepods. J. Exp. Mar. Biol. Ecol. **123**: 1–14. doi:10.1016/0022-0981(88)90105-0

Dam, H. G., M. R. Roman, and M. J. Youngbluth. 1995. Downward export of respiratory carbon and dissolved inorganic nitrogen by diel-migrant mesozooplankton at the JGOFS Bermuda time-series station. Deep-Sea Res. Part I **42**: 1187–1197. doi:10.1016/0967-0637(95)00048-B

De Robertis, A. 2002. Size-dependent visual predation risk and the timing of vertical migration: An optimization model. Limnol. Oceanogr. **47**: 925–933. doi:10.4319/lo.2002.47.4.0925

Ducklow, H. W., D. K. Steinberg, and K. O. Buesseler. 2001. Upper ocean carbon export and the biological pump. Oceanography **14**: 50–58. doi:10.5670/oceanog.2001.06

Evans, G. T., and J. S. Parslow. 1985. A model of annual plankton cycles. Biol. Oceanogr. **3**: 327–347. doi:10.1080/01965581.1985.10749478

Frangoulis, C., E. D. Christou, and J. H. Hecq. 2005. Comparison of marine copepod outfluxes: Nature, rate, fate and role in the carbon and nitrogen cycles. Adv. Mar. Biol. **47**: 253–309. doi:10.1016/S0065-2881(04)47004-7

Giering, S. L., and others. 2014. Reconciliation of the carbon budget in the ocean's twilight zone. Nature **507**: 480–483. doi:10.1038/nature13123

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: Test of a model with foraging minnows. Ecology **68**: 1856–1862. doi:10.2307/1939877

Hays, G. C. 1996. Large-scale patterns of diel vertical migration in the North Atlantic. Deep-Sea Res. Part I **43**: 1601–1615. doi:10.1016/S0967-0637(96)00078-7

Hays, G. C., C. A. Proctor, A. W. G. John, and A. J. Warner. 1994. Interspecific differences in the diel vertical migration of marine copepods: The implications of size, color, and morphology. Limnol. Oceanogr. **39**: 1621–1629. doi:10.4319/lo.1994.39.7.1621

Heywood, K. J. 1996. Diel vertical migration of zooplankton in the Northeast Atlantic. J. Plankton Res. **18**: 163–184. doi:10.1093/plankt/18.2.163

Hirst, A.G., and T. Kiørboe. 2002. Mortality of marine planktonic copepods: global rates and patterns. Mar Ecol.: Prog. Ser. **230**: 195–209.

Honjo, S., and M. R. Roman. 1978. Marine copepod fecal pellets—production, preservation and sedimentation. J. Mar. Res. **36**: 45–57.

Houston, A. I., J. M. McNamara, and J. M. Hutchinson. 1993. General results concerning the trade-offs between gaining energy and avoiding predation. Philos. Trans. R. Soc. B **341**: 375–397. doi:10.1098/rstb.1993.0123

Houston, A. I., and J. M. McNamara. 1999. Models of adaptive behaviour: An approach based on state. Cambridge Univ. Press.

Irigoien, X., D. V. Conway, and R. P. Harris. 2004. Flexible diel vertical migration behaviour of zooplankton in the Irish Sea. Mar. Ecol.: Prog. Ser. **267**: 85–97. doi:10.3354/meps267085

Jónasdóttir, S. H., A. W. Visser, K. Richardson, and M. R. Heath. 2015. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. Proc. Natl. Acad. Sci. U.S.A. **112**: 12122–12126. doi:10.1073/pnas.1512110112

Kiørboe, T., and H. Jiang. 2013. To eat and not be eaten: Optimal foraging behaviour in suspension feeding copepods. J. R. Soc. Interface **10**: 20120693. doi:10.1098/rsif.2012.0693

Kristiansen, T., C. Jørgensen, R. G. Lough, F. Vikebø, and Ø. Fiksen. 2009. Modeling rule-based behavior: Habitat selection and the growth-survival trade-off in larval cod. Behav. Ecol. **20**: 490–500. doi:10.1093/beheco/arp023

Lenz, J., A. Morales, and J. Gunkel. 1993. Mesozooplankton standing stock during the North Atlantic spring bloom study in 1989 and its potential grazing pressure on phytoplankton: A comparison between low, medium and high latitudes. Deep-Sea Res. Part II **40**: 559–572. doi:10.1016/0967-0645(93)90032-I

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Can. J. Zool. **68**: 619–640. doi:10.1139/z90-092

Longhurst, A. R. 1976. Vertical migration, p. 116–137. *In* D. H. Cushing and J. J. Walsh [eds.], The ecology of the seas. Blackwell Scientific Publications.

Longhurst, A. R., and W. G. Harrison. 1989. The biological pump: Profiles of plankton production and consumption in the upper ocean. Prog. Oceanogr. **22**: 47–123. doi:10.1016/0079-6611(89)90010-4

Longhurst, A. R., A. Bedo, W. G. Harrison, E. Head, and D. Sameoto. 1990. Vertical flux of respiratory carbon by oceanic diel migrant biota. Deep-Sea Res. Part I **37**: 685–694. doi:10.1016/0198-0149(90)90098-G

Mangel, M., and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton Univ. Press.

Martin, J. H., G. A. Knauer, D. M. Karl, and W. W. Broenkow. 1987. VERTEX: Carbon cycling in the northeast Pacific. Deep-Sea Res. Part I **34**: 267–285. doi:10.1016/0198-0149(87)90086-0

Mauchline, J. 1998. The biology of calanoid copepods, V. **33**. Academic Press.

Morales, C. E. 1999. Carbon and nitrogen fluxes in the oceans: The contribution by zooplankton migrants to active transport in the North Atlantic during the joint global ocean flux study. J. Plankton Res. **21**: 1799–1808. doi:10.1093/plankt/21.9.1799

Sainmont, J., U. H. Thygesen, and A. W. Visser. 2013. Diel vertical migration arising in a habitat selection game. Theor. Ecol. **6**: 241–251. doi:10.1007/s12080-012-0174-0

Sainmont, J., A. Gislason, J. Heuschele, C. N. Webster, P. Sylvander, M. Wang, and Ø. Varpe. 2014. Inter- and intra-specific diurnal habitat selection of zooplankton during the spring bloom observed by Video Plankton

Recorder. Mar. Biol. **161**: 1931–1941. doi:10.1007/s00227-014-2475-x

Sainmont, J., K. H. Andersen, U. H. Thygesen, Ø. Fiksen, and A. W. Visser. 2015. An effective algorithm for approximating adaptive behavior in seasonal environments. Ecol. Modell. **311**: 20–30. doi:10.1016/j.ecolmodel.2015.04.016

San Martin, E., R. P. Harris, and X. Irigoien. 2006. Latitudinal variation in plankton size spectra in the Atlantic Ocean. Deep-Sea Res. Part II **53**: 1560–1572. doi:10.1016/j.dsr2.2006.05.006

Sanders, R., S. A. Henson, M. Koski, and others. 2014. The biological carbon pump in the North Atlantic. Prog. Oceanogr. **129**: 200–218. doi:10.1016/j.pocean.2014.05.005

Sarmiento, J. L., T. M. Hughes, R. J. Stouffer, and S. Manabe. 1998. Simulated response of the ocean carbon cycle to anthropogenic climate warming. Nature **393**: 245–249. doi:10.1038/30455

Sheldon, R., and T. Parsons. 1967. A continuous size spectrum for particulate matter in the sea. J. Fish. Res. Board Can. **24**: 909–915. doi:10.1139/f67-081

Smith, K. L., H. A. Ruhl, B. J. Bett, D. S. M. Billett, R. S. Lampitt, and R. S. Kaufmann. 2009. Climate, carbon cycling, and deep-ocean ecosystems. Proc. Natl. Acad. Sci. U. S. A. **106**: 19211–19218. doi:10.1073/pnas.0908322106

Steinacher, M., and others. 2010. Projected 21st century decrease in marine productivity: A multi-model analysis. Biogeosciences **7**: 979–1005. doi:10.5194/bg-7-979-2010

Steinberg, D. K., C. A. Carlson, N. R. Bates, S. A. Goldthwait, L. P. Madin, and A. F. Michaels. 2000. Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. Deep-Sea Res. Part I **47**: 137–158. doi:10.1016/S0967-0637(99)00052-7

Steinberg, D. K., E. F. Horgan, and L. P. Madin. 2001. Zooplankton at the Bermuda Atlantic Time-Series study (BATS) station: Diel, seasonal and interannual variation in biomass, 1994-1998. Deep-Sea Res. Part II. **48**: 2063–2082. doi:10.1016/S0967-0645(00)00171-5

Steinberg, D. K., S. A. Goldthwait, and D. A Hansell. 2002. Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. Deep Sea Res., Part I **49**: 1445–1461.

Steinberg, D. K., J. Cope, S. E. Wilson, and T. Kobari. 2008a. A comparison of mesopelagic mesozooplankton community structure in the subtropical and subarctic North Pacific Ocean. Deep-Sea Res. Part II **55**: 1615–1635. doi:10.1016/j.dsr2.2008.04.025

Steinberg, D. K., B. A. Van Mooy, K. O. Buesseler, P. W. Boyd, T. Kobari, and D. M. Karl. 2008b. Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. Limnol. Oceanogr. **53**: 1327–1338. doi:10.4319/lo.2008.53.4.1327

Stukel, M. R., M. D. Ohman, C. R. Benitez-Nelson, and M. R. Landry. 2013. Contributions of mesozooplankton to vertical carbon export in a coastal upwelling system. Mar. Ecol.: Prog. Ser. **491**: 47–65. doi:10.3354/meps10453

Townsend, D. W., L. M. Cammen, P. M. Holligan, D. E. Campbell, and N. R. Pettigrew. 1994. Causes and consequences of variability in the timing of spring phytoplankton blooms. Deep-Sea Res. Part I **41**: 747–765. doi:10.1016/0967-0637(94)90075-2

Visser, A. W. 2007. Motility of zooplankton: Fitness, foraging and predation. J. Plankton Res. **29**: 447–461. doi:10.1093/plankt/fbm029

Volk, T., and M. I. Hoffert. 1985. Ocean carbon pumps: Analysis of relative strength and efficiencies of in ocean-driven circulation atmospheric CO_2 changes, p. 99–110. *In* E. T. Sundquist and W. S. Broecker [eds.], The carbon cycle and atmospheric CO_2: Natural variation archean to present. American Geophysical Union.

Ward, B. A., S. Dutkiewicz, O. Jahn, and M.J. Follows. 2012. A size-structured food-web model for the global ocean. Limnol. Oceanogr. **57**: 1877–1891. doi:10.4319/lo.2012.57.6.1877

Wiebe, P. H., N. J. Copley, and S. H. Boyd. 1992. Coarse-scale horizontal patchiness and vertical migration of zooplankton in Gulf Stream warm-core ring 82-H. Deep-Sea Res. Part I **39**: 247–278. doi:10.1016/S0198-0149(11)80015-4

Acknowledgments

We would like to thank Ken Haste Andersen for inputs and discussion during the development of this study. This work was funded by the Danish Council for Strategic Research under the North Atlantic–Arctic Coupling in a Changing Climate: Impacts on Ocean Circulation, Carbon Cycling and Sea-Ice (NAACOS), The European Union Seventh Framework Programme Basin Scale Analysis, Synthesis and Integration (ENV.2010.2.2.1-1; www.euro-basin.eu), and The Centre for Ocean Life, a VKR Centre of excellence supported by the Villum Foundation.

Submitted 2 June 2015
Revised 22 October 2015
Accepted 19 November 2015

Associate editor: Ronnie Glud